

GLAUCODON BALLARATENSIS (MARSUPIALIA, DASYURIDAE), A LATE
PLIOCENE 'DEVIL' FROM BATESFORD, VICTORIA.

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The right mandible of a dasyurid from Pliocene sediments at Batesford, near Geelong, Victoria is described as a new specimen of *Glaucodon ballaratensis* Stirton, 1957. The new specimen is morphologically close to the holotype of *Glaucodon ballaratensis*. Several dental characteristics of the new specimen unknown from the holotype of *Glaucodon ballaratensis* are close to those of *Sarcophilus moornaensis* Crabb, 1982. *Glaucodon ballaratensis* also shares features with *Dasyurus maculatus* Kerr, 1792 and *Sarcophilus lamiarhus harrisii* Bôitard, 1842, and hence the Batesford specimen offers additional information on the origins of these dasyurids.

Key words: *Glaucodon ballaratensis*, Pliocene, Batesford, Moorabool Viaduct Sands, Dasyuromorphia, Dasyuridae.

THE DASYUROMORPHIAN fossil record represents the dominant marsupial insectivore-carnivore radiation in Australasia during the Quaternary. Discoveries from Late Oligocene and Miocene deposits in Riversleigh in northwestern Queensland have extended this record (Wroe, 1998), and Wroe (2003) provides a modern summary of fossil Dasyuromorphian record. However, the order is poorly represented in the Pliocene, where the species *Glaucodon ballaratensis* Stirton, 1957, *Dasyurus dmmalli* Bartholomai, 1971, *Archerium chinchillaensis* Wroe & Maekness 2000 and *Sarcophilus moornaensis* Crabb, 1982 are the only known dasyuromorphians. The Pliocene record may also include indeterminate species of *Antechinus* from Grange Burn, Victoria (Turnbull & Lundelius, 1970), and *Planigale* from Bluff Downs in Queensland (Archer, 1982).

The monotypic genus *Glaucodon* was described by Stirton (1957) and based on a single right mandible with the M4 present. The holotype was found in the Parish Well at Smeaton, near Ballarat. The specimen was originally presented to the National Museum of Victoria in 1914 by Mr. J. Marshall, and remained undescribed for over forty years. E. D. Gill revisited the type location and discovered the first molar (M1) which fits into the alveolus and contacts perfectly with the broken root of the posterior alveolus (Gill, 1953). The holotype of *Glaucodon ballaratensis* (NMV

P16136) therefore includes the remains collected by both Marshall and Gill. In 1964, W. D. Turnbull recognised two fragments in the Museum Victoria Vertebrate Palaeontology Collections as coming from the well at Smeaton that belonged to the holotype of *G. ballaratensis*. Together the fragments provide much of the outline of the ascending ramus from the left dentary. This material was not available to Stirton (1957) when the holotype was first described.

Stirton did not assign *G. ballaratensis* a geological age with any certainty. Gill's analysis of the sediments surrounding the supplementary material collected in 1953 indicated that the specimen's stratigraphical position in the section at Smeaton can be established relative to the overlying basalt flows (Gill, 1953). Another analysis of the Smeaton locality undertaken in 1993 noted that the fossiliferous layer that contained *G. ballaratensis* lies above a basalt flow which correlates closely with a nearby flow with a radiometric date of 2.1 myBP (Turnbull, Lundelius & Tedford, 1993). Basalt flows above the fossiliferous layer have been interpreted as no older than 1.9 myBP (Aziz-ur-Rhman & McDougall, 1972). This implies that the sediment containing *G. ballaratensis* represents an interval between basalt flows of the ages of 1.9 myBP and 2.1 myBP, which implies a Late Pliocene age for the holotype.

The right mandible of a fossil dasyurid with near complete dentition (NMV P207018) was presented to

the Museum of Victoria in 1996 by Mr. P. Robertson. Robertson's specimen was found in the Moorabool Viaduct Sands (Pliocene) outcropping at Portland Cement Limited's Limestone quarry at Batesford, Victoria. The specimen was referred to *G. ballaratensis* (T. H. Rich, pers. comm. 1997, see Gerdzt, 2001). Morphological characteristics of the teeth of this specimen fully confirm that the specimen belongs to this species. Measurements and comparisons of the teeth and mandible of Robertson's specimen reveal differences in relative proportions of the molar trigonids and mandibular depth to those of the holotype, however the differences are considered to be of infraspecific importance.

The significance of *G. ballaratensis* in dasyuromorphian evolution has been discussed by Gill (1953), Stirton (1957), Ride (1964), Marshall (1973), Archer (1976, 1982), Archer and Bartholomai (1978) and Crabb (1982). Characteristics of the Batesford specimen offer additional information on the phylogeny of the Dasyuridae, specifically the relationship of *Glaucodon* to *Dasyurus maculatus* Kerr, 1792, *Sarcophilus laniarius harrisi* Boitard, 1842 and *Sarcophilus moornaensis* Crabb, 1982.

STRATIGRAPHY AND AGE OF THE BATESFORD SPECIMEN

It has been suggested (T. H. Rich, pers. comm.) that the distinctive preservation of the Batesford specimen of *G. ballaratensis* indicates that it was originally located in a fissure filling within the argillaceous Moorabool Viaduct Sands of Pliocene age. The unit, as exposed at Batesford Quarry, consists of a black, silty clay with a notable absence of finely comminuted marine fossils (Rich, 1976). The dark brown coloration of the mandible and black coloration of the tooth enamel of the specimen corresponds with other vertebrate remains attributed to this unit, notably a *Zygomaturus* sp. mandible found in these sediments at Batesford in 1975 (Rich, 1976). This unit has yielded a substantial list of fossilized remains known as the Dog Rocks Local Fauna, including marsupials and other mammals such as Rodentia (Muridae), along with representatives of Osteichthyes (Teleostei), Amphibia (Anura), Reptilia (Squamata), and Aves (Rich, 1991).

The sediments of this unit indicate a fluvial environment existed to the southeast of the Dog Rocks during the Pliocene. It is the characteristic preservation of the Dog Rocks local fauna, along with information

provided on the location of the new specimen by Robertson that led T. H. Rich to his assessment that the specimen came from this setting. The fossiliferous unit of the Moorabool Viaduct Sands was overlain by a number of basalt flows of the Newer Volcanics (Bowler, 1963). Three kilometres to the south of Batesford Quarry, a magnetically reversed flow with similar petrographic characteristics was dated at 2.03 +/- 0.13 my BP in three different samples (Aziz-ur-Rahmen & McDougall, 1972). A determination for the maximum age of the fluvial sediments was provided by the foraminiferan *Globorotalia crassiformis*, which first appeared at 4.0 myBP (Whitelaw, 1989) and occurs in the sediments of the Moorabool Viaduct Sand stratigraphically below the fissures. In these sediments, the magnetic orientation is reversed (Whitelaw, 1989) which suggests that the age of the fissures is within the interval of 4.0 and 1.9 myBP, thus placing it in either the early Matuyama Chron (2.48-2.03 myBP) or the late Gilbert Chron (4.88-3.40 myBP) (Aziz-ur-Rahmen & McDougall, 1972). The presence of rodents in the local fauna such as the two identified *Pseudomys* species suggests that the early Matuyama Chron is the most likely interval represented in these sediments (Whitelaw, 1989).

SYSTEMATIC PALAEOLOGY

Subclass MARSUPIALIA Illiger, 1811

Cohort AUSTRALIDELPHIA Szalay, 1982

Order DASYUROMORPHIA Gill, 1872

Family DASYURIDAE Goldfuss, 1820

Genus *Glaucodon* Stirton, 1857

Type species *Glaucodon ballaratensis* Stirton, 1857

Holotype. The diagnostic features of the holotype of *G. ballaratensis* (NMV P 16136) were defined as the following: Molar row length intermediate between *Dasyurus maculatus* and *Sarcophilus laniarius harrisi*; gross morphology of mandible less robust than *Sarcophilus* form but more so than *D. maculatus*; M4 length of 10.0 mm +/- 0.1 mm; M4 width 6.7 mm +/- 0.4 mm; M1 length 7.2 mm +/- 0.5 mm; M1 width 4.3 mm +/- 0.2 mm (Stirton, 1957).

The dental morphology of the holotype of *G. ballaratensis* (NMV P16136) has been discussed by

Gill (1953), Stirton (1957), Ride (1964), Marshall (1973), Archer (1976, 1982), Areher and Bartholomai (1978), Crabb (1982) and Long et al. (2002). It was fully described by Stirton (1957) based on a solitary right mandible with M1 and M4 present, and alveoli for M2, M3, P1, P2, C, and an incomplete row of incisor alveoli. Gill (1953) postulated in his field notes, but did not formally describe, the specimen as a member of the genus *Sarcophilus*. *G. ballaratensis* is regarded herein as a morphologically intermediate form between *Sarcophilus laniarius harrisii* and *Dasyurus maculatus*, displaying characteristics referable to both species. Stirton (1957) also noted some dental morphological similarities between *G. ballaratensis* and *Dasyurus viverrinus* (Shaw, 1800), however the similarities were less marked than those of *D. maculatus*.

***Glaucodon ballaratensis* Stirton, 1957**

Fig. 1, 2, 3

Sarcophilus? Gill, 1953, p. 87

Glaucodon ballaratensis Stirton, 1957, p. 129-133, text-figure 6.

Glaucodon ballaratensis Stirton, 1957, - Areher, 1984, p. 634, Table 1; p. 635, fig 2; p. 639, fig 17; p. 640, fig. 18; . Pl. 6.7-1. - Crabb, 1982, p. 514 - 515, fig 4, - Areher, 1982, p. 409, fig 7, p. 417. - Ride, 1964, p. 109, fig 8; Long et al., 2002, p. 55, fig p. 53 (mislabelled as *Dasyurus dunnalli*)

New material. NMV P207018. As for *G. ballaratensis* holotype (NMV P16136), with the following additional features: Mandible with four molars (M1, M2, M3 and M4) in situ, however the protoconid of M4 is absent, possibly due to

Fig. 1. NMVP 207018, occlusal view. Scale bar intervals represent 10mm.



postmortem abrasion. Also present are two well-spaced premolars (P2 and P3) and a large crescentic canine. Occlusal surfaces are relatively unworn, suggesting that the specimen was a young adult. The mandible of the specimen is somewhat shorter and more robust than holotype.

Locality of new material. Specimen found by P. Robertson in the Moorabool Viaduct Sand, a member of the Brighton Group (Pliocene), at Portland Cement Limited's limestone quarry at Batesford, Geelong, Victoria (38° 6.5' S., 144° 17.5' E).

Diagnosis of species. Diagnostic features are: deep, channel-like precingulum extending to the parastylid on M2, M3 and M4 (precingulum on M1 present but less markedly) consistent with 'bone cracking' dasyurids; more robust trigonids than holotype (M1 trigonid longer, M4 trigonid both longer and wider); crowding of molar row out of line comparable to holotype (and *S. moornaensis*, but significantly less than *S. lanarius harrisii*); talonid-like notch in ante-

rior base of P2 undercuts and is rectilinear to the protoconid, premolar diastema intermediate between *D. maculatus* and *S. lanarius harrisii* and referable to alveoli on *G. ballaratensis* holotype; P1 significantly lower than P2 with rounded, low cusp. The mandible is more robust and deeper than holotype, deepest beneath the M4 between roots.

Measurements were taken from twenty specimens each of *D. maculatus* and *S. lanarius harrisii*, as well as the holotypes of *S. moornaensis* (NMV P28684) and *G. ballaratensis* (NMV P16136) to provide a morphometric comparison of twenty-eight dental and mandibular characteristics against the new specimen (Table 1). Measurements from the canine are discarded as being diagnostic because of wear via occlusion. The parameters of variability of the measurements of the talonid and trigonid basins of the M2 and M3 are not used as a diagnostic feature from the holotype, as these teeth are represented by alveoli only.

NMV P207018 differs from the holotype of *G. ballaratensis* in the following characteristics: more robust mandible, mandibular depth beneath P2 deeper

Fig. 2. NMVP 207018, lingual view. Scale bar intervals represent 10mm.



and closer to the mandibular depth proportions displayed in *S. moornaensis*, M1 and M4 wider.

NMV P207018 shares the following features with the holotype: molar talonids weaker and more adpressed than *Sarcophilus*, but less so than *Dasyurus*, molar protoconids high and sharp, particularly on M3 and inferred on M4, molar row length and crowding intermediate between *S. moornaensis* and *D. maculatus*.

It has been suggested that Robertson's specimen may represent an ontogenetically older individual of *G. ballaratensis* (G. D. Sanson, pers. comm., 1999). Whilst this addresses the apparent crowding of the molar row of the illustrated specimen (as a result of interstitial wear), the occlusal wear patterns on the protoconid and the hypoconid of the M1 of NMV P 207018, unknown to Sanson, suggest it was of similar or younger ontogenetic age than the holotype. The observed differences in dental morphology between the two specimens, however, provide insufficient evidence for the existence of two species of *Glaucodon*.

Morphometric analyses set forth by Simpson, Roe

& Lewontin (1960) were used by Marshall (1973) to synonymise *G. ballaratensis* with a specimen from the Moorna Sands, South Australia. This diagnosis was later re-examined by Crabb (1982) using morphological observations, and the Moorna Sands specimen was erected as the holotype of *Sarcophilus moornaensis*. This suggests that Simpson's form of analysis is problematic when morphological observations are not included in the statistical analysis. It is pertinent to note that data derived from Simpson's approach implied the presence of two species of *Glaucodon* on the basis of dental measurements (Table 2) when comparing the *Glaucodon* specimens.

The present authors consider that it is therefore necessary to incorporate both observations of morphology and dental measurement statistics concurrently to diagnose this species from other morphologically similar taxa.

Description of NMV P207018. Dentition more complete than holotype (NMV P16136), however, ramus length and length of molar row is marginally shorter,

Fig. 3. NMV P207018, labial view. Scale bar intervals represent 10mm.



CHARACTER	<i>Dasyurus maculatus</i> (n) = 20	<i>Sarcophilus launiarus harrisi</i> (n) = 20	<i>Sarcophilus moornaensis</i> (n) = 1	<i>G. ballaratensis</i> holotype MV P16136 (n) = 1	<i>G. ballaratensis</i> MV P702018 (n) = 1
Length of molar series	27.7 +/- 3.8	44 +/- 4.7	38.5	36.4	35
M1 length	7.7 +/- 2.1	9.2 +/- 2.6	7.8	7.4	6.5
M1 width	3.7 +/- 1	6.2 +/- 2.5	5.2	4	4.5
M1 trigonid length	2.7 +/- 1.2	7 +/- 3.2	7.2	4.3	4.7
M1 trigonid width	1.8 +/- 0.8	4.5 +/- 1.7	5	4.3	4.3
M1 talonid width	2.1 +/- 1	4.9 +/- 2.2	3.2	4.5	4.3
M2 length	6.5 +/- 1.7	10.9 +/- 2.9	9.5	absent	8.6
M2 width	3.4 +/- 1	6.5 +/- 1.8	5.9	absent	4.8
M2 trigonid length	3.3 +/- 1.3	8.4 +/- 2	8.7	absent	6.1
M2 trigonid width	3.4 +/- 1.2	5.2 +/- 3.7	3.8	absent	4.9
M2 talonid width	3.1 +/- 1	3.3 +/- 1.8	4.5	absent	5.2
M3 length	6.7 +/- 2.2	12 +/- 2.7	10	absent	9.8
M3 width	3.9 +/- 1.9	7.4 +/- 1.5	6.3	absent	6.7
M3 trigonid length	3.6 +/- 1.8	7.7 +/- 1.8	8	absent	7.6
M3 trigonid width	3.6 +/- 1.4	5.6 +/- 1.4	5.4	absent	5.2
M3 talonid width	2.8 +/- 1.2	2.3 +/- 2.1	3.3	absent	4.4
M4 length	6.8 +/- 2.3	11.9 +/- 3.6	11.2	10	10.1
M4 width	3.7 +/- 1.6	6.5 +/- 2.1	6.5	5.8	6.3
M4 trigonid length	4.4 +/- 1.3	9.9 +/- 1.2	10.2	6	8.2
M4 trigonid width	3.7 +/- 1.2	4.8 +/- 1.4	4.6	3.3	5.6
M4 talonid width	2.9 +/- 1	2.3 +/- 1.8	2.9	2	2.1
P2 length	4.2 +/- 1.7	6 +/- 2.7	absent	absent	4.3
P2 width	3.2 +/- 1.3	6.7 +/- 2.3	absent	absent	3.5
P3 length	4.9 +/- 2.1	6.7 +/- 2	absent	absent	5.9
P3 width	2.9 +/- 1.1	6.5 +/- 2.2	absent	absent	3.9
Mandible depth below P2	10.6 +/- 2.3	12.4 +/- 3.4	14.6	10.1	12.2
Mandible depth below M4	15.1 +/- 3.1	12.3 +/- 2.8	20	17.5	17.1
Mandible depth below M1	14.1 +/- 3.8	13.8 +/- 3	14.7	13.7	13

Table 1. Mean dental measurements from subjective and comparative material

incisor alveolus not present due to incomplete preservation of specimen. Premolars in line with significant spacing, canine relatively robust and crescentic. P1 is set oblique to antero - posterior axis of tooth row and P2 is only slightly so. Molars characterized by deep, channel-like precingulum extending to the parastylid.

M1 short but wide; heavy median protoconid; anterior median crest from base to top of protoconid; metaconid tightly adpressed to posterolingual slope of protoconid; hypoconid massive and slightly crescentic; hypoconulid in postcromedian position at posterior end of hypoconid crescent; entoconid as small rounded cusp; talonid basin with narrow lingual opening anterior and posterior to entoconid - no direct posterior opening; posterior lower labial corner extends farther posteriorly than other parts of the tooth; trigonid long and deep; paraconid obscure due to massive nature of protoconid.

M2 with moderate paraconid - protoconid shear; protoconid higher than paraconid, separated by carnassial notch; protoconid with posteriorly oriented curvature, inner lingual surface flattened; metaconid much lower than protoconid but only marginally shorter than paraconid; talonid basin comparatively large, high and shallow with wider lingual opening posterior to entoconid and small posterior opening; margin of talonid with entoconid only marginally lower than hypoconid; posterior lower labial corner marginally extends further posteriorly than other parts of the tooth; trigonid basin high and shallow.

M3 with high sharp paraconid - protoconid shear; protoconid higher than paraconid, separated by carnassial notch along paracristid; protoconid high with crescentic distally oriented curve, noticeable groove along labial aspect of metacristid; metaconid lower than protoconid but roughly the same height as paraconid; protoconid higher than paraconid.

M4 wide; protoconid absent, possibly due to abrasion; remains of high paraconid - protoconid shear surface evident; partial protoconid and paraconid separated by a carnassial notch in the paracristid; metaconid lower than paraconid; trigonid basin wide and shallow. The trigonid length compared to the total length of the molar is large, and is a characteristic of this species not shown in the comparative material of *D. maculatus*, *S. harrisi* and *S. moornaensis*.

Paraconid and metaconid progressively enlarge from M2 to M4, however talonid remains adpressed in each case. Remains of the incomplete M4 protoconid suggests it was higher than paraconid with marginally adpressed talonid present.

P2 composed of single high anterior cusp with angular posterior slope to mandible attachment longer than anterior slope; anterior attachment to mandible separated by notch in base in line with single high cusp. P1 much lower than P2; cusp barely discernible on worn surface; anteriorly well spaced from P2 but crowded in line with C.

C high and crescentic; slight lingual slope; single rounded high cusp; anteriolingual surface marked by vertical groove.

Discussion of phylogeny of Glauconodon Considerable discussion on the phylogeny of *Glauconodon* exists. Marshall (1973, p. 156) considered that there was an absence of morphological differences between *G. ballaratensis* and *S. moornaensis*, and hence synonymised the two species. The methodologies of Simpson, Roe & Lewontin (1960) were applied as a basis of dental morphometric analysis in this instance. While there are distinct morphological similarities between *Glauconodon* and *Sarcophilus*, specimens of the latter are larger and more robust, with a significantly greater mandibular depth and crowding of the molar row.

Ride (1964) proposed that *G. ballaratensis* was structurally ancestral to *S. harrisi*, but in some characteristics closer to larger species of *Dasyurus* such as *D. maculatus*. This suggestion implies *Glauconodon* is ancestral to *Sarcophilus* with some characteristics referable to *Dasyurus*. The phylogenetic relationships of *Dasyurus* and *Sarcophilus* have been established by molecular studies indicating that the genera form a monophyletic group (Krajewski et al., 1994). It is noteworthy that more recent molecular data is not in accord with this interpretation (Krajewski et al., 2000), but more recent morphology-based numerical parsimony supports the case for monophyly of this taxa (Wroe et al., 2000). This demonstrates the significance of morphology in the elucidation of phylogeny in extant taxa. Archer and Bartholomai (1978, p. 5) recognized "a structural lineage starting with a hypothetical fossil form similar to *D. maculatus*, to *G. ballaratensis*, to the annectant extinct species of *Sarcophilus* and ending with *S. harrisi* is one of the best documented marsupial structural phylogenies", where the annectant species mentioned is *S. moornaensis*. Wroe (1998) discussed the phylogeny of this lineage from the perspective of an ancestral Miocene dasyurid, *Ganbulanyi djadjinguli* Wroe, 1998, noting synapomorphies of *Dasyurus*, *Glauconodon* and *Sarcophilus*.

Crabb (1982) considered the lower molars of *S.*

moornaensis similar to (and as apomorphic as) the molars of *G. ballaratensis*. The mandibular depth and crowding of the molar row of *S. moornaensis* is greater than that of both specimens of *Glaucodon*, however this characteristic is less marked in the Batesford specimen. The more robust trigonids of the M1 and M4 and the mandibular depth of the Batesford specimen differ from the *G. ballaratensis* holotype, however these differences are regarded as being of infraspecific importance. It is important to consider, when discussing the relationships of the *Glaucodon*-*Dasyurus*-*Sarcophilus* lineage, the relative ages of all the taxa involved. *S. moornaensis* is considered Early Pleistocene in age (Long et al., 2002). The revised estimation of the geological age of the holotype of *G. ballaratensis* (2.0 myBP \pm 0.1 myBP) removes the importance of the specimen in 'stage-of-evolution' correlation for this group of dasyurids, as the occurrence of the species is too recent to constitute 'common ancestry' (Turnbull, Lundelius & Tedford, 1993). However, the morphology of the teeth attributed herein to *G. ballaratensis* combined with the estimated geological age of NMV P207018 (2.2 myBP \pm 0.25 myBP) raises the significance on the species in terms of 'stage-of-evolution' correlation. *G. ballaratensis* can now be regarded as representing a collateral lineage to *Sarcophilus*. The retention of characteristics such as the gracile mandibular form shared by *Glaucodon* and *Dasyurus* are considered symplesiomorphic.

The dental and mandibular characteristics of NMV P207018 provide new data on *Glaucodon* and the characteristics that it shares with *Sarcophilus*. *G. ballaratensis* is a Pliocene form that, whilst sufficiently different to warrant generic distinction from

the Dasyurinae and *Sarcophilus*, has characteristics aligning it with these taxa. The molar row crowding and proportions of the M4 trigonid of NMV P207018 implies a closer affinity between the genera *Glaucodon* and *Sarcophilus* than previously postulated. The poorly developed molar talonids of NMV P207018 align the specimen with *Glaucodon* rather than *Sarcophilus*. The robust molars of the Batesford specimen are morphologically intermediate between the holotype of *G. ballaratensis* and *S. moornaensis*. However, these differences are likely to represent intraspecific variation within *G. ballaratensis* rather than a new species of *Glaucodon*.

A possible interpretation of the phylogeny of the lineage is as follows: at some point prior to the late Pliocene, the Dasyurinae diversified resulting in the origin of the *Sarcophilus*-*Glaucodon* lineage. The plesiomorphic gracile morphology and uneroded molars of the ancestral form were retained and are present in extant species of *Dasyurus*. The *Sarcophilus*-*Glaucodon* lineage retained some elements of the dental arrangement of the ancestral form. However, significant progressive crowding of the molar row is an evident apomorphy of the subfamily as displayed in *S. lanianus harrisi*.

Glaucodon branched from the *Sarcophilus*-*Glaucodon* lineage after the split from the Dasyurinae, but prior to the occurrence of *S. moornaensis*. *G. ballaratensis* arose at some point prior to the Late Pliocene, and retained the symplesiomorphic proportions present in the mandible of *D. maculatus*, but also displayed characteristics which unite it with *Sarcophilus*. A characteristic of *Sarcophilus* is the gradual increase of morphological robustness through the Plio-Pleistocene *S. moornaensis* to the massively

CHARACTER	<i>G. ballaratensis</i> holotype MV P 16136	<i>G. ballaratensis</i> MV P 702018	Log. difference	Nearest whole number value for V	Indicative of new species ?
Length of molar series	34.4	35	0.0076	<1	N
M1 Length	7.4	6.5	0.056	3 to 4	Y
M1 Width	4	4.5	0.0511	3 to 4	Y
M1 Trigonid length	4.4	4.7	0.029	1 to 2	N
M1 Trigonid width	4.3	4.3	nil	N/A	N
M1 Talonid width	4.5	4.3	0.03	1 to 2	N
M4 Length	10	10.1	0.004	<1	N
M4 Width	5.8	6.3	0.0359	2 to 3	N
M4 Trigonid length	6	8.2	0.1356	7 to 8	Y
M4 Trigonid width	3.3	5.6	0.2297	12 to 13	Y
M4 Talonid width	2	2.1	0.0212	1 to 2	N
Mandible depth below P2	10.1	12.2	0.082	4 to 5	Y
Mandible depth below M4	17.3	17.1	0.0051	<1	N
Mandible depth below M1	13.5	13.2	0.0097	<1	N

Table 2. Application of morphometric analysis of Simpson et al. (1960) to *Glaucodon*. (Note: values for V greater than 3 indicate a different species. Chronology and phylogeny are not applied in this approach to species differentiation.)

robust *S. lanianus* complex of the Pleistocene. Future discoveries from these theorised lineages could add to the understanding of the evolution of the Dasyuridae in the Plio-Pleistocene.

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REFERENCES

- ARCHER, M., 1976. The dasyurid dentition and its relationships to that of didelphids, thylacynids, borhyaenids (Marsupicarnivora) and peremelids (Peremelina: Marsupialia). *Australian Journal of Zoology, Supplementary Series*, 39: 1-34
- ARCHER, M., 1982. Review of the Dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. In *Carnivorous Marsupials Vol. 2*, Archer, M., ed. Royal Zoological Society of New South Wales, Sydney.
- ARCHER, M., & CLAYTON, G. (eds) 1984. *Vertebrate Zoogeography & Evolution in Australasia (Animals in Space and Time)*, Hesperian Press, Victoria Park.
- ARCHER, M. & BARTHOLOMAI, A., 1978. Tertiary mammals of Australia: A synoptic view. *Aleheringa* 2: 1-20.
- AZIZ-UR-RAHMAN, & MCDUGALL, I., 1972. Potassium-Argon ages on the New Volcanics of Victoria. *Proceedings of the Royal Society of Victoria* 85: 61-9.
- BOITARD, P., 1842. *Le Jardin des Plantes a Paris. Description et moeurs des Mammiferes de la Menagerie et du Museum d'Histoire Naturelle/ precede d'un introduction historique, descriptive et pittoresque par M. J. Janin*. Paris: J.J. Dubochet et Ce, i-lxvi, 472 pp.
- BOWLER, J. M., 1963. Tertiary Stratigraphy and Sedimentation in the Geelong - Maude area, Victoria. *Proceedings of the Royal Society of Victoria* 76: 7-137, Pls. 15-18.
- CRABB, P. L., 1982. Pleistocene dasyurids (Marsupialia) from south western New South Wales. In *Carnivorous Marsupials. Vol. 2*, M. Archer, M., ed. Royal Zoological Society of New South Wales, Sydney. 511-516.
- GERDTZ, W. R., 2001. McCoy and *Sarcophilus harrisii* Boitard, 1842 - a Diabolical Relationship. *The Victorian Naturalist* 118 (5), 231-233.
- GILL, E. D., 1953. Distribution of the Tasmanian Devil, the Tasmanian Wolf and the Dingo in southeast Australia in Quaternary time. *The Victorian Naturalist* 70: 86-90.
- GILL, T., 1872. Arrangement of the Families of Mammals: with analytical tables. Prepared for the Smithsonian Institution by Theodore Gill. *Smithsonian miscellaneous collections*; Volume 9, article 1, number 230, 1-98.
- GOLDFUSS, G. A., 1820. Thl. 3 Handbuch der Zoologie. In *Handbuch dner Naturgeschichte: zum Gebrauch bei Vorlesungen*. G. H. von Schubert. Nurenburg.
- ILLIGER, J. K. W., 1811. C. Illigeri ...*Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione Germanica*. Berolini.
- KERR, R., 1792. *The Animal Kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; Class I. Mammalia, containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copper plates*. London: J. Murray & R. Faulder, Part 1, xi + 400 pp. 9 pls.
- KRAJEWSKI, C., PAINTER, J., BUCKLEY, L. & WESTERMAN, M., 1994. Phylogenetic structure of the marsupial family Dasyuridae based on Cytochrome - DNA sequences. *Journal of Mammalian Evolution* 2 25-35.
- KRAJEWSKI, C., WROE, S. & WESTERMAN, M., 2000. Molecular evidence for the pattern and timing of cladogenesis in dasyurid marsupials. *Zoological Journal of the Linnean Society*, 130: 375-404.
- LONG, J., ARCHER, M., FLANNERY, T. & HAND, S.,

2002. *Prehistoric Mammals of Australia and New Guinea: One Hundred Million Years of Evolution*. University of New South Wales Press Ltd, University of New South Wales, Sydney.
- MARSHALL, L. G., 1973. Fossil vertebrate faunas from the Lake Victoria region, S. W. New South Wales, Australia. *Memoirs of the National Museum of Victoria* 34: 151-81.
- OWEN, R. In T. L. Mitchell, 1838. *Three expeditions into the interior of eastern Australia, with descriptions of the recently explored region of Australia Felix, and of the present colony of New South Wales*. T & W Boone, London.
- OWEN, R., 1877. *Researches on the fossil remains of the extinct mammals of Australia; with a notice on the extinct marsupials of England*, Volumes 1 & 2. J. Erxleben, London.
- RICH, T. H., 1976. Recent fossil discoveries in Victoria. *Victorian Naturalist* 93(5): 198-206.
- RICH, T. H., 1991. Australia's mammal record. In *Vertebrate Palaeontology of Australasia*, P. Vickers-Rich, J.M. Monaghan, R. F. Baird, & T. H. Rich, eds. Monash University Publishing Committee, Melbourne, 893-1070.
- RIDE, W. D. L., 1964. A review of the Australian fossil marsupials. *Journal of the Proceedings of the Royal Society of Western Australia*. 47: 97-131.
- SHAW, G., 1800. *General Zoology or systematic natural history: Quadrupeds*. G. Kearsley, London, Vol. 1, Pt 2, i-viii, 249-552.
- SIMPSON, G. G., ROE, A. & LEWONTIN, R. C., 1960. *Quantitative Zoology*. Harcourt, Brace & World Publishing Inc., New York.
- STIRTON, R. A. 1957. Tertiary Marsupials from Victoria, Australia. *Memoirs of the National Museum of Victoria* 21: 121-134.
- SZALAY, F. S., 1982. A new appraisal of marsupial phylogeny and classification. In *Carnivorous Marsupials Volume 2*, M. Archer ed., Surrey Beauty & Sons Pty. Ltd. and The Royal Zoological Society of New South Wales, Mosman, 621-640.
- TURNBULL, W. D. & LUNDELIUS, E. L. fil., 1970. The Hamilton Fauna: A late Pliocene mammalian fauna from the Grange Burn, Victoria, Australia. *Fieldiana Geology* 19: 1-163.
- TURNBULL, W. D., LUNDELIUS, E. L. fil. & TEDFORD, R. H., 1993. Fossil vertebrate locality at Smeaton, Victoria. *Memoirs of the Association of Australasian Palaeontologists* 15: 429-440.
- WIITELAW, M. J., 1989. Magnetic polarity stratigraphy and Mammalian fauna of the late Pliocene (Early Matayuma) section at Batesford, Victoria. *Journal of Geology* 97: 11-24.
- WROE, S., 1998. A new 'bone-cracking' dasyurid (Marsupialia) from the Miocene of Riversleigh, northwestern Queensland. *Alcheringa* 22: 277-284.
- WROE, S., 2003. Australian marsupial carnivores: an overview in recent advances in palaeontology. In M. Jones, C. Dickman, & M. Archer, eds. *Predators with Pouches: The biology of Carnivorous Marsupials*, CSIRO Publishing, Melbourne, 102-123.
- WROE, S., EBACH, M., AIYONG, S., MUIZON, C. de, & MUIRHEAD, J., 2000. Cladistic analysis of dasyuromorphian (Marsupialia) phylogeny using cranial and dental features. *Journal of Mammalogy*, 81: 1008-1024.
- WROE, S., & MACKNESS, B. S., 2000. A new genus and species of dasyurid from the Pliocene Chinchilla Local Fauna of south-eastern Queensland. *Alcheringa* 24: 319-326.

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